PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
109(2):397–405. 1996.

Late Eocene entelodonts (Mammalia: Artiodactyla) from Inner Mongolia, China

Spencer G. Lucas and Robert J. Emry

(SGL) New Mexico Museum of Natural History and Science,
1801 Mountain Road N.W., Albuquerque, New Mexico 87104, U.S.A.;
(RJE) Department of Paleobiology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Abstract.—Previously undescribed specimens of *Entelodon* from the late Eocene (Ergilian) of Nei Monggol, China represent two species, small and large. We identify the small species as *Entelodon gobiensis* (Trofimov, 1952), because this is the oldest valid name available for a relatively small species of Asian *Entelodon. E. diconodon* (Trofimov, 1952) is a nomen dubium, and it is probable that *E. ordosius* (Young & Chow, 1956), *E. major* Biryukov, 1961 and *E. orientalis* Dashzeveg, 1965 are junior subjective synonyms of *E. gobiensis* (Trofimov, 1952). The large species is *Entelodon dirus* Matthew & Granger, 1923, a species previously known only from its holotype M3, but to which we now refer a lower jaw with p2–m3. In Asia, *Entelodon* is more common in strata of Ergilian (late Eocene) age; its Shandgolian (early Oligocene) occurrences are few. Entelodonts originated in Asia during the middle Eocene, immigrated to North America (late Eocene) and Europe (early Oligocene) and persisted until late Oligocene in Eurasia and North America. The last entelodonts, from the early Miocene of North America, apparently arose from a separate, latest Oligocene emigration from Asia.

Entelodonts were a family of Eocene-Miocene giant suiform artiodactlys, some with skulls nearly one meter long. They are especially well represented in the fossil record in western North America (Peterson 1909) and western Europe (Brunet 1979). In Asia, the oldest entelodonts (*Eoentelodon*) are of middle Eocene (Irdinmanhan) age, and the group persisted until the late Oligocene. The genus *Entelodon* is known from the late Eocene (Ergilian) to early Oligocene (Shandgolian), and two genera, *Paraentelodon* and *Neoentelodon,* are of late Oligocene (Tabenbulukian) age. In this article, we describe a sample of *Entelodon* from the late Eocene of Nei Monggol (Inner Mongolia), China (Fig. 1), and clarify the taxonomy of the Asian species of *Entelodon* in Asia. We use the Asian "land mammal age" terminology (e.g., Irdinmanhan, Ergilian, Shandgolian) as it was established by Russell & Zhai (1987).

Abbreviations used.—When used in dental notations upper case letters denote upper (skull) teeth and lower case letters denote lower (dentary) teeth. Institutional abbreviations used are: AMNH—American Museum of Natural History, New York; IVPP—Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; KAN—Kazakh Academy of Sciences, Almaty; MAN—Mongolian Academy of Sciences, Ulan Bator; PIN—Paleontological Institute of the Russian Academy of Sciences, Moscow.

Systematic Paleontology

Family Entelodontidae Lydekker, 1883
Genus *Entelodon* Aymard, 1847

Fig. 1. Map of *Entelodon* localities in Asia. 1, Houldjin, Baron Sog and Urtyn Obo formations, Nei Monggol, China; 2, Cajiachong Formation, Yunnan, China; 3, Ergilin Dzo svita, Mongolia; 4, Kusto svita, Zaysan basin, Kazakhstan; 5, Iwaki Formation, Japan; 6, Chilikta svita at Kursay near Lake Chelkar Teniz, Kazakhstan; 7, Qingshuiying Formation, Lingwu, Ningxia, China; 8, "indricothere" svita at Dulygaly-Zhilanchik, Kazakhstan.

Entelodon gobiensis (Trofimov, 1952)
Figs. 2B, D, 3A–C

Referred specimens.—From the Baron Sog Formation at Nom Khong Obo, Holy Mesa, Nei Monggol, China: AMNH 26184, lower jaw with left and right p3 (Fig. 2B–D).

From the Baron Sog Formation at Urtyn Obo, East Mesa, Suiyuan, Nei Monggol, China: AMNH 26176, skull fragments and left and right I1–M3 (Fig. 3A–B).

From the Houldjin Formation 7 miles west of Camp Margetts, Nei Monggol, China: AMNH field number 839, right M3 (Fig. 3C).

Description.—The upper dentition of AMNH 26176 merits description as one of the best preserved upper dentitions of *Entelodon* from Asia. The I1 is an almost conical tooth with a very convex labial side, less convex lingual side and a prominent lingual cingulum. Measurements (in mm) are: length = 16.7; width = 14.6. The I2 is a larger, more caniniform tooth missing the base of the crown, so comparable measurements cannot be obtained. The I3 is a recurved tooth, with the crown more triangular in cross section than that of the I1 or I2. It is very convex labially and has a lingual cingulum. Length = 26.8, width = 22.5. The canine is a recurved tooth similar to the I3 but lacks the base of the crown.

The P1 is dominated by a single cusp,

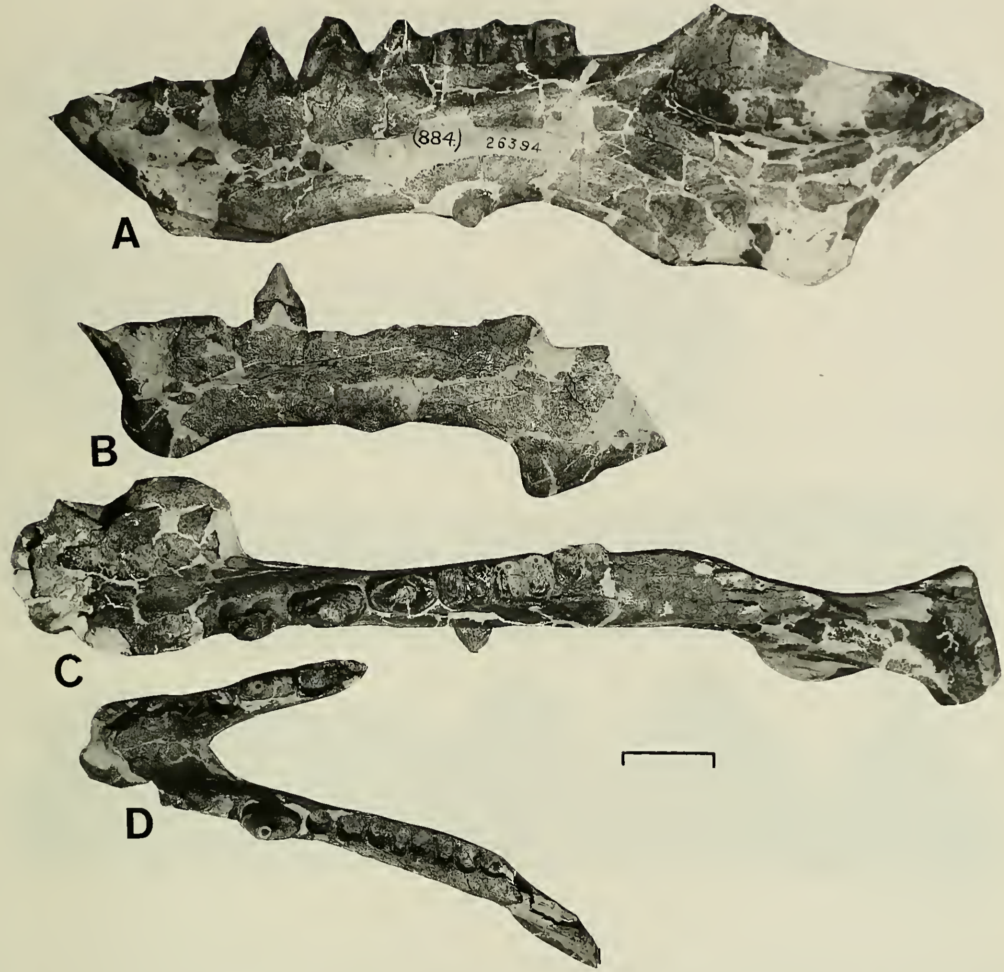

Fig. 2. Lower jaws of *Entelodon* from the upper Eocene of Nei Monggol, China. A, C, *E. dirus,* AMNH 26394, lower jaw with left p2–m3, in lateral (A) and occlusal (C) views. B, D, *E. gobiensis,* AMNH 26184, lower jaw with left and right p3, in lateral (B) and occlusal (D) views, negative reversed for easier comparison. Bar scale = 5 cm.

the paracone. The crown is curved slightly linguad. The labial face of the tooth is convex, and a ridge extends from the anterior end of the tooth to the apex of the paracone and then to the posterior base of the crown. Length = 22.2, width = 10.8.

The P2 is a larger version of P1 except that the paracone is not as lingually deflected, and it has a cingulum around the entire crown: on the labial face, beneath the paracone, the cingulum is only weakly developed. Like the P1, P2 is a trenchant tooth with two roots, one positioned anteriorly and the other posteriorly. Length = 32.8, width = 16.9.

The P3 has a triangular crown dominated by the paracone, which is deflected slightly linguad. It has a prominent posterior ridge and a less prominent anterior ridge. The basal cingulum is essentially continuous around the crown. One large root is present anteriorly, and there are two fused roots posteriorly. Length = 36.9, width = 25.6.

The crown of P4 is subtriangular in oc-

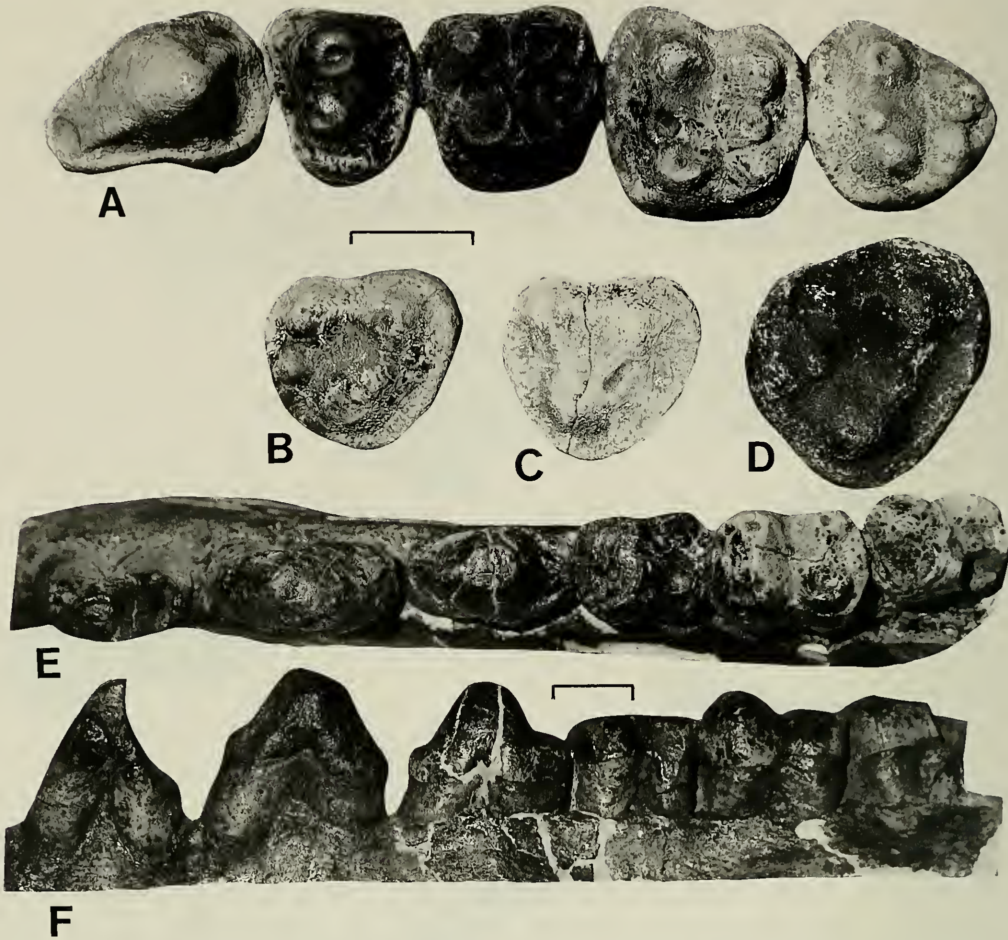

Fig. 3. Cheek teeth of *Entelodon* from the upper Eocene of Nei Monggol, China. A–B, *E. gobiensis,* AMNH 26176, occlusal view of left P3–M3 (A) and right M3 (B). C, *E. gobiensis,* AMNH field number 839, occlusal view of right M3. D, *E. dirus,* AMNH 19181 (holotype), occlusal view of right M3. E–F, *E. dirus,* AMNH 26394, occlusal (E) and labial (F) views of left p2–m3. Bar scales = 2 cm.

clusal outline, with its longer axis oriented transversely. There is a large paracone with an equally large, closely appressed protocone. A basal cingulum is prominent on the anterior, lingual and posterior margins of the tooth, and is present but weaker labially. There is a faint suggestion of a parastyle, and a convex ectoloph. The tooth has three divergent roots. Length = 25.5, width = 29.6.

The m1 is approximately square, with subequal paracone, metacone, protocone and hypocone. The anterior cingulum is prominent. The labial cingulum is faintly developed and a tiny mesostyle is present. The well worn condition of this tooth results in two lophs, one connecting the paracone and the protocone, and the other the metacone and the hypocone. A strong posthypocone crista is confluent with the posterior cingulum. It has two divergent roots labially and two fused roots lingually. For measurements of M1–M3, see Table 1.

The M2 is subrectangular in occlusal outline, and is substantially larger than M1. It also differs from M1 in having distinct

Table 1.—Measurements (in mm) of selected upper and lower cheek teeth of *Entelodon* from Asia. L = maximum antero-posterior length; W = maximum transverse width.

Specimen	M1L	M1W	M2L	M2W	M3L	M3W
E. gobiensis						
AMNH 26176	29	31	33	34	31	31
AMNH "839"					32	29
IVPP V825.1[a]	31	32				
KAN 31-181/54T[b]	28	32	33	36	29	32
MAN 27-1[c]	25	27	30	34	27	30
MAN 27-2[d]	29	31	33	37		
PIN 473-256[e]	25	32	31	39		
E. dirus						
AMNH 19181[f]						

Specimen	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
E. gobiensis								
AMNH "839"			28	23				
IVPP V2926.1[g]			27	21	31	25	29	21
KAN 32-181/54T[h]	40	21	29	23	31	27	33	25
KAN 35(29)3837[i]	38	20	27	21	31	26	31	24
PIN 473-129[j]					35	29		
PIN 478-126[j]					32	24		
PIN 478-287[k]	32	17						
E. dirus								
AMNH 26394	41	22	33	25	38	29	33	25

[a] Holotype of *E. ordosius* (Young & Chow, 1956), [b] Holotype of *E. major* Biryukov, 1961; [c] Holotype of *E. orientalis* Dashzeveg (1965); [d] Referred specimen of *E. orientalis*; [e] Holotype of *E. gobiensis* (Trofimov, 1952); [f] Holotype of *E. dirus* Matthew & Granger, 1923; [g] Referred specimen of *E. ordosius*; [h] Holotype of *E. major* Biryukov, 1961; [i] Measurements from Emry et al. (1996); [j] Referred specimen of *E. gobiensis*; [k] Holotype of *E. diconodon* (Trofimov, 1952).

para- and metaconules, a relatively larger anterior cingulum, and a more distinct labial cingulum.

The M3 is subtriangular in occlusal outline. Its anterior part is very much like that of M2, but the posterior loph is much narrower, and lacks the metaconule. The metacone is deflected linguad. The hypocone is small but retains a posterior crista confluent with the posterior cingulum.

The lower jaw is represented by AMNH 26184. Its horizontal ramus is of nearly equal depth throughout and bears two tubercles, one beneath the p1 and anterior alveolus of p2, and the other beneath the anterior part of m1. The anterior tubercle is a convex eminence that is inclined laterally so that the horizontal ramus dorsal to it is convex laterally. The posterior tubercle is a blunt swelling that projects ventrolaterally. Two small mental foramina are on the lateral surface of the horizontal ramus, one under p1 and the other under the anterior alveolus of p3. The anteroventral aspect of the mandibular symphysis is a broad, nearly flat, sloping surface. Spacing of the alveoli of the canine and anterior premolars indicates that no diastemata separate these teeth. The canine alveolus is large, trihedral in cross section and opens anteriorly and dorsally nearly parallel to the inclination of the symphysis. The p1 alveolus is a single cavity; its cross section is ovoid with the long axis anteroposteriorly oriented. The p2 has two separate alveoli, both circular in cross section, the posterior much the larger of the two. The p3 is a trenchant tooth with a tall, pointed cuspid followed posteriorly by a short heel. The p3 is two-rooted, as were p4-m3, judging from their alveoli.

Discussion.—Brunet (1979) did much to revise the taxonomy of Asian entelodonts at the generic level. A species-level revision is overdue, and we offer some observations toward one.

Trofimov (1952) named *Entelodon diconodon* for a right p4 (he misidentified it as a left p2: Brunet 1979) from Kursay near Lake Chelkar-Teniz in Kazakhstan (Fig 1, No. 6). The paratype is a right m2 from the same locality. These specimens cannot be distinguished metrically or morphologically from those of other small *Entelodon* species from Asia or from some European *Entelodon,* although p4 is relatively smaller (Table 1) and has an accessory cuspid on the posterior slope of the trigonid, unlike other specimens. We agree with Brunet (1979) that *E. diconodon* should be considered a *nomen dubium.*

Trofimov (1952) named *Brachyodon gobiensis* for a partial skull with badly damaged left P1-M3 from Ergilin-Dzo in Mongolia. Trofimov (1958) replaced the preoccupied name *Brachyodon* with the name *Ergilobia.* Brunet (1979) synonymized *Ergilobia* with *Entelodon.* The type specimen is poorly preserved, but metrically it cannot be distinguished from the other relatively small specimens of Asian *Entelodon* (Table 1).

Young & Chow (1956, p. 41, fig. 4, pl. 1, figs. C–D) named *Archaeotherium ordosius* for an M1 (IVPP V 825.1) from Lingwu, Ningxia. They diagnosed the species by its large size and brachyodont, sexitubercular upper molar with a prominent accessory cusp on the labial cingulum. According to Young & Chow (1956), IVPP V 825.1 is indistinguishable from the M1 of *Archaeotherium* except for its larger size. However, Brunet (1979) argues that this tooth more closely resembles that of *Entelodon,* especially in its heavy labial cingulum, and created the new combination *Entelodon ordosius* for it. Nevertheless, the size and morphology of the holotype of *E. ordosius* do not distinguish it from other small *Entelodon* from Asia (Brunet 1979).

Hu (1964) referred lower jaw fragments from Urtyn Obo, Nei Monggol, to *A. ordosius.* The bilophodonty of the lower molars justify assignment to *Entelodon* (Brunet 1979). In size and morphology, these teeth cannot be distinguished from other Asian small specimens of *Entelodon* (Table 1).

Biryukov (1961) based a new species *E. major* on a skull and lower jaw from Dulygaly-Zhilanchik in Kazakhstan. This is by far the most informative type specimen of any species of *Entelodon* from Asia, but it closely resembles in size and morphology all the other names species except *E. dirus* and *E. diconodon.* Biryukov's diagnosis of *E. major* stressed its large size, massive skull, flared-out suborbital flanges, infraorbital foramen above P4, short I3-C and C-P1 diastemata, internal choanae (palatine notch) at the level of the posterior end of M3, and upper sexitubercular upper molars whose crowns are wider than long. These are features of the genus *Entelodon,* and neither these characters nor size differentiate *E. major* from the other relatively small Asian *Entelodon.*

Dashzeveg (1965) described *E. orientalis* on the basis of a left maxillary fragment with M1–3, from Khoer-Dzan, Mongolia. His diagnosis emphasized large size, low crowned and sexitubercular upper molars with anterior and posterior cingula, M3 with a protoconule but lacking a metaconule, and palatine notch at the level of the middle of M3. These features and size (Table 1) do not, however, distinguish the holotype, or the referred specimens, of *E. orientalis* from other small specimens of *Entelodon* from Asia.

It thus seems likely that only one small species of *Entelodon* is known in Asia. *Entelodon gobiensis* (Trofimov 1952) is the oldest available and valid name for that species, given that *E. diconodon* is a *nomen dubium. Entelodon ordosius* (Young & Chow 1956), *E. major* Biryukov, 1961 and *E. orientalis* Dashzeveg, 1965 are probably junior subjective synonyms of *E. gobiensis* (Trofimov, 1952). The specimens of *E. gobiensis* reported here are the first records of *Entelodon* from the Baron Sog Formation of Nei Monggol.

Entelodon dirus Matthew & Granger, 1923
Figs. 2A, C, 3D–F

Holotype.—AMNH 19181, right M3 (Fig. 3D)

Horizon and locality of holotype.—Houldjin Formation, 3 mi. (4.8 km) southwest of Iren Dabasu, Nei Monggol, China.

Referred specimens.—From the Houldjin Formation at Overnight Camp, Camp Margetts area, Nei Monggol, China: AMNH 26394, incomplete lower jaw with p2–m3 (Figs. 2A, C, 3E–F).

From the Houldjin Formation 7 miles (11.2 km) west of Camp Margetts, Nei Monggol, China: AMNH field number 36, two canine fragments; field number 839, left p2 and right m1.

Description.—The lower jaw has a flat, sloping, plate-like symphysis. This orientation gives the I1–3 a slightly procumbent flare. The anterior tubercle is a crest or ridge that begins under the canine and continues to beneath the p2–3. The posterior tubercle is a blunt spike under the m1–2 juncture. Judging from the sizes of alveoli, i1 < i2 < i3 < c. The canine alveolus is much larger than that of i3 and is round in cross section. The p1 has a single alveolus, with the cross section an antero-posteriorly elongate oval. There are no diastemata between the teeth.

The p2 is a two-rooted, trenchant tooth dominated by a large paraconid. The p3 is a similar trenchant tooth. Both p2 and p3 have a discontinuous cingulid across the lingual face of the paraconid. The p4 has a talonid and accessory cuspid on the postero-lingual base of the paraconid slope. The p2–4 are inclined slightly posteriad.

The m1 is subrectangular in occlusal outline. With advancing wear it becomes slightly bilophodont. The m2 is a larger version of m1, with more distinct lophids, a well developed hypoconulid and a labial cingulid. The m3 is well worn but similar to m2, though it is smaller and has a relatively smaller talonid.

Discussion.—Prior to this report, *E. dirus* was known only from its holotype M3. The lower jaw, AMNH 26394, is from the same stratigraphic level as the holotype, and is from a nearby locality. It is too large to belong to *E. gobiensis* (Table 1), and its m3 is of appropriate size to occlude with the holotype M3 of *E. dirus,* to which we assign it.

Biochronology and Paleobiogeography

Entelodon occurs in Asia in strata of late Eocene (Ergilian) and early Oligocene (Shandgolian) age. The Ergilian occurrences are: (1) Houldjin, Baron Sog and Urtyn Obo formations, Nei Monggol, China (Matthew & Granger 1923, Hu 1964, this paper); (2) Cajiachong Formation, Yunnan China (Wang & Zhang 1983); (3) Ergilin Dzo svita, Mongolia (Trofimov 1952, Dashzeveg 1976); (4) Kusto svita, Zaysan basin, Kazakhstan (Emry et al. 1996); and (5) Iwaki Formation, Japan (Tomida 1986). The Shandgolian occurrences are: (1) Chilikta svita at Kursay near Lake Chelkar-Teniz, Kazakhstan (Trofimov 1952); (2) Qingshuiying Formation, Lingwu, Ningxia, China (Young & Chow 1956); and (3) "indricothere" svita at Dulygaly-Zhilanchik, Kazakhstan (Biryukov 1961). *Entelodon* is much more common and widespread in Ergilian strata than in Shandgolian strata.

The oldest and most primitive known entelodont is *Eoentelodon* from the middle Eocene (Irdinmanhan) Xiangshan and Lumeiyi formations of Yunnan, China (Chow 1958; Zhang et al. 1978). The genus has been reported from strata as young as late Eocene (Ergilian) in Mongolia (Dashzeveg 1965). Entelodonts first appear in North America during the Eocene (Duchesnean) in the form of *Brachyhyops* (Lucas 1992), and first appear somewhat later in Europe, during the early Oligocene (Brunet 1979). In Europe, the subsequent diversification of entelodonts was modest and relatively short lived. In North America, entelodonts became fairly diverse and abundant during the late Eocene and early Oligocene (Chadronian-Orellan) (Effinger 1987). They declined through the later Oligocene, and at about the end of the Oligocene a reentry from Asia gave rise to the giant entelodonts of the North American early Miocene. The known record of Asian entelodonts suggests that in Asia their diversity remained low, being limited to middle-late Eocene *Eoentelodon,* late Eocene-early Oligocene *Entelodon* and two genera of late Oligocene age, *Neoentelodon* from the Aktau svita of eastern Kazakhstan (Aubekerova 1969) and *Paraentelodon* from the Pestrotsvet svita at Benara, Georgia (Gabuniya 1964).

Given the temporal and geographic distribution of entelodonts and the authors' concept of their phylogeny (to be published in detail elsewhere), we agree with Brunet (1979) that entelodonts arose in Asia during the middle Eocene. They subsequently emigrated to North America in the late Eocene and to Europe in the early Oligocene. The immigrants gave rise to separate North American and European diversifications during the early Oligocene. Entelodonts persisted in Asia, North America and Europe through the Oligocene, but became extinct in North America and Europe late in the epoch. They emigrated again from Asia to North America at about the end of the Oligocene to produce the last entelodont, *Ammodon,* of the early Miocene.

Acknowledgments

The National Geographic Society and the Smithsonian Institution's Charles D. Walcott Fund supported this research. R. Tedford allowed us to study specimens in the AMNH collections. We thank P. Holroyd and C. Ray for their helpful reviews.

Literature Cited

Aubekerova, P. A. 1969. Novyy predstavitel' semeystva Entelodontidae.—Izvestiya Akademiya Nauk Kazakhskoy SSR Seriya Biologicheskiy 4:47–52.

Aymard, A. 1847. Essai monographique sur un nouveau genre de mammifere fossil trouvé dans la Haute-Loire et nommé *Entelodon.*—Annales de la Société d'Agriculture, Sciences, Arts et Commerce du Puy 12:227–267.

Biryukov, M. D. 1961. Entelodont (Entelodontidae) iz sredneoligotsenovykh otlozheni verkhovyev Zhilanshika.—Akademiya Nauk Kazakhskoi SSR Institut Zoologii Materialy po istorii fauny i flori Kazakhstana 3:11–19.

Brunet, M. 1979. Les grands mammif res chefs de file de l'immigration Oligocene et le probleme de la limite Éocene-Oligocene en Europe.—Éditions de la Fondation Singer-Polignac, Paris 281 pp.

Chow, M.-c. 1958. *Eoentelodon,* a new primitive entelodont from the Eocene of Lunan, Yunnan.—Vertebrate PalAsiatica 2:30–36.

Dashzeveg, D. 1965. *Entelodon orientalis* n. sp. (Suiformes) from the Oligocene of the Gobi Desert, Mongolia.—Acta Paleontologica Polonia 10: 281–285.

———. 1976. Novyye dannyye of Entelodontidae (Artiodactyla, Suiformes) iz Oligotsena Mongoli.—Sovmestnaya Sovestkovo-Mongoloskaya Paleontologicheskaya Ekspeditsiya Trudy 3:47–50.

Effinger, J. A. 1987. Systematics and paleobiology of White River Group Entelodontidae (Mammalia, Artiodactyla).—Unpublished M.S. Thesis, South Dakota School of Mines and Technology, Rapid City, South Dakota, 150 pp.

Emry, R. J., S. G. Lucas, & B. U. Bayshashov. 1996. Early Oligocene entelodont from the Zaysan basin, northeastern Kazakhstan.—Selevinia, in press.

Gabuniya, L. K. 1964. Benarskaya fauna oligotsenovykh pozvonochnykh.—Akademiya Nauk Gruzinskoy SSR Institut Paleobiologii Izdatelstvo "Metsnierba," Tbilisi, 268 pp.

Hu, C. 1964. *Archaeotherium ordosius* from Oligocene of Inner Mongolia.—Vertebrate PalAsiatica 8:312–317.

Lucas, S. G. 1992. Redefnition of the Duchesnean land mammal "age." late Eocene of western North America. Pp. 88–105 *in* D. R. Prothero & W. A. Berggren, eds., Eocene-Oligocene climatic and biotic evolution. Princeton University Press, 568 pp.

Lydekker, R. 1883. Siwalik selenodont Suinae.—Paleontologica Indica, series 10(2):146.

Matthew, W. D., & W. Granger. 1923. The fauna of the Houldjin Gravels.—American Museum Novitates 97:1–6.

Peterson, O. A. 1909. A revision of the Entelodontidae.—Memoirs of the Carnegie Museum 4:41–158.

Russell, D. E., & R. Zhai. 1987. The Paleogene of Asia: mammals and stratigraphy.—Mémoires du Muséum National d'Historie Naturelle, Sciences de la Terre 52:488 pp.

Tomida, Y. 1986. Recognition of the genus *Entelodon* (Artiodactyla, Mammalia) from the Joban Coalfield, Japan, and the age of the Iwaki Formation.—Bulletin of the National Science Museum, Series C, 12:165–170.

Trofimov, B. A. 1952. Novyye entelodontidy iz Mongolii i Kazakhstana.—Akademiya Nauk SSR Trudy Paleontologicheskiy Institut 41:144–154.

———. 1958. On a new name for the entelodont *Brachyodon* Trofimov, 1952, *Ergilobia* nom. nov.—Materialy k osnovam paleontologii 2: 119.

Wang, B., & Y. Zhang. 1983. New finds of fossils from Paleogene of Qujing, Yunnan.—Vertebrata PalAsiatica 21:119–128.

Young, C. C., & M.-c. Chow. 1956. Some Oligocene mammals from Lingwu, N. Kansu.—Acta Paleontologia Sinica 4:337–460.

Zhang, Y., W. Huang, T. Tang, H. Ji, Y. You, Y. Tong, S. Ding, X. Huang, & J. Zheng. 1978. The Cenozoic of the Lantian region, Shaanxi Province.—IVPP Memoir 14:64 pp.